

Environmental characteristics of ephemeral rock pools explain local abundances of the clam shrimp, *Paralimnadia badia* (Branchiopoda: Spinicaudata: Limnadiidae)

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ABSTRACT

The conditions of ephemeral freshwater pools are highly variable through time, and their inhabitants must be able to tolerate these changing conditions to survive. Although much research has focused on large branchiopod hatching requirements, there is comparatively little information available on the environmental conditions endured by adult clam shrimp populations. A suite of physical and chemical characteristics, especially pool depth, influence the presence or absence of clam shrimp populations in rock pools on granite outcrops in the Wheatbelt region of Western Australia. Here we examine multiple environmental variables of temporary rock pools and how they may affect adult populations of the clam shrimp, *Paralimnadia badia*.

KEYWORDS: habitat, physiochemical, temporary pool, pool morphology, hydroperiod, environmental variability

INTRODUCTION

Clam shrimp are branchiopod crustaceans (Branchiopoda: Spinicaudata) that are obligate dwellers of temporary waters (Dumont & Negrea 2002). Populations survive dry periods in the form of resting eggs produced by mature females or hermaphrodites. Their eggs lie dormant until appropriate conditions are met for hatching (Brendonck 1996, Brendonck & Riddoch 2000, Brendonck & De Meester 2003). Upon inundation, a fraction of resting eggs hatch, leaving behind a bank of dormant eggs in the sediment (Brendonck 1996, Brendonck & De Meester 2003). Occasionally, eggs will continue to hatch even after the initial inundation, resulting in multiple generations of shrimp in a single pool (Benvenuto *et al.* 2009). Often, rain will fill the pool and eggs will hatch but not reach sexual maturity before the basin dries. In these instances, the egg bank is vital to ensure long-term population persistence (Brendonck & De Meester 2003). In this way shrimp 'hedge their bets' against the unpredictability of their environment which has led to speculation as to which factors might promote this pattern of hatching (Mossin 1986, Brendonck *et al.* 1996, Kuller & Gasith 1996, Simovich & Hathaway 1997, Beladjal *et al.* 2007).

Many physical environmental parameters, including dissolved oxygen, pH, osmotic pressure, light, and temperature, have been individually implicated in

regulating hatching in various large branchiopod species (Bishop 1967, Belk 1977, Scott & Grigarick 1979, Mitchell 1990, Schönbrunner & Eder 2006). However, initial hatching conditions are not sole predictors of clam shrimp presence, as temporary pool environmental conditions change throughout the duration of their inundation and drying regimes (Jocqué *et al.* 2007a). Here we aim to determine environmental factors that are associated with maintenance of adult populations of clam shrimp.

For a hatched population to be sustained, the conditions of the pool must meet survival requirements after initial hatching. Long term maintenance of populations of several species of *Daphnia* have been assessed in relation to habitat characteristics and each species appeared to thrive under different environmental conditions, occupying different pools as a result (Pajunen & Pajunen 2007). Both the size and permanence (length of hydroperiod) of temporary pools have been found to play important roles in predicting species richness (Kiflawi *et al.* 2003). Additionally, since larger pools will resist evaporation for longer periods of time, pool size has been shown as an important factor structuring local communities (Jocqué *et al.* 2007b).

Our study sought to answer how temporary pool environments relate to adult clam shrimp populations. Here we determine which parameters best explain abundances of adult populations of the clam shrimp *Paralimnadia badia* (Wolf 1911; the Australian species *Limnadia* have recently been moved to a new endemic genus *Paralimnadia*, Rogers *et al.* 2012) in a variety of temporary rock pools on granite outcrops in the semi-arid, Wheatbelt region of Western Australia.

⁴Deceased March 2013

METHODS

Study Sites

Although the Wheatbelt region of southwestern, Western Australia is generally flat, occasional large granite outcrops (or 'inselbergs' *sensu stricto*, Withers 2000) can be found in the area (York Main 1997, Withers 2000). The rainy season in this part of Australia lasts approximately from May to October and is the milder time of the year, with mean maximum air temperatures ranging from 20.3°C to 23.7°C (Commonwealth of Australia, Bureau of Meteorology, 26 Sept 2011).

Three outcrops received adequate rainfall for sustained hydration: Holland Rock (Shire of Kent, 33°21.259'S; 118°44.639'E; 13 pools sampled), Dingo Rock (Shire of Lake Grace, 33°0.558'S; 118°36.321'E; 8 pools sampled), and Rockhole Rock (Shire of Bruce Rock, 31°55.970'S; 117°45.209'E; 11 pools sampled). Data from Bruce Rock were collected at a later date than Holland and Dingo (May 2009) and were only used to construct Fig. 3.

Field Sampling

Study pools were selected for a range of sizes and depths, and were sampled for physiochemical parameters and quantities of clam shrimp and other macroinvertebrates in late April to late May 2007. Water quality [temperature, pH, dissolved oxygen (DO), and electrical conductivity (EC)] of each of the three sites was monitored for five consecutive days at four times per day (12:00, 14:00, 16:00, and 18:00) to assess diurnal change, however for most analysis only the average of the mid-afternoon readings (14:00 and 16:00) were used as a result of incomplete sampling across the other two time periods. Pools on Holland and Dingo Rocks were sampled with a YSI 556 multi-probe (YSI, USA). Pools on Rockhole Rock were sampled with a Hydrolab Quanta multi-parameter meter (Hydrolab, USA). Pool dimensions measured included maximum length (l), maximum width (w) and mean depth (d) (each averaged from three measurements). Pool volumes were estimated from these dimensions assuming the shape to be half of an ellipsoid (Formula: $4/3\pi lwd$, Baron *et al.* 1998).

Each pool was sampled across the entire volume for three, 3-min periods with sweep nets of mesh sizes 2.0 mm and then 0.5 mm. *Paralimnadia badia* abundance approximately halved each sampling event over the three successive rounds of sampling. Consequently, after three rounds in each pool approximately 90% of clam shrimp had been captured. *Paralimnadia badia* were sorted from other macroinvertebrates in white plastic collecting trays, species were identified, counted, and then returned to the pool alive.

Analysis of habitat variables and species distributions

Volume and EC values were \log_{10} transformed to achieve normality. All other variables had normally distributed residuals (using Shapiro-Wilk test for normality). One-way ANOVAs compared the means of environmental variables between pools with and without *P. badia*.

All parametric analyses were made with JMP Pro 10 (SAS Institute Inc. 2012). Ordinations of environmental

data were produced by Principal Components Analysis (PCA) in PRIMER multivariate software (PRIMER-E 2006). Although not suitable for analysis of biotic community structure, the implicit underlying Euclidean Distance matrix of this method makes it suitable for environmental data, with an advantage over nMDS ordination in that ordination axes are interpretable (Clarke & Warwick 2001). Correlations between pairs of environmental variables were then examined with draftsman plots. Combinations of highly correlated variables (Spearman rank higher than 95%) were reduced to a single, representative variable.

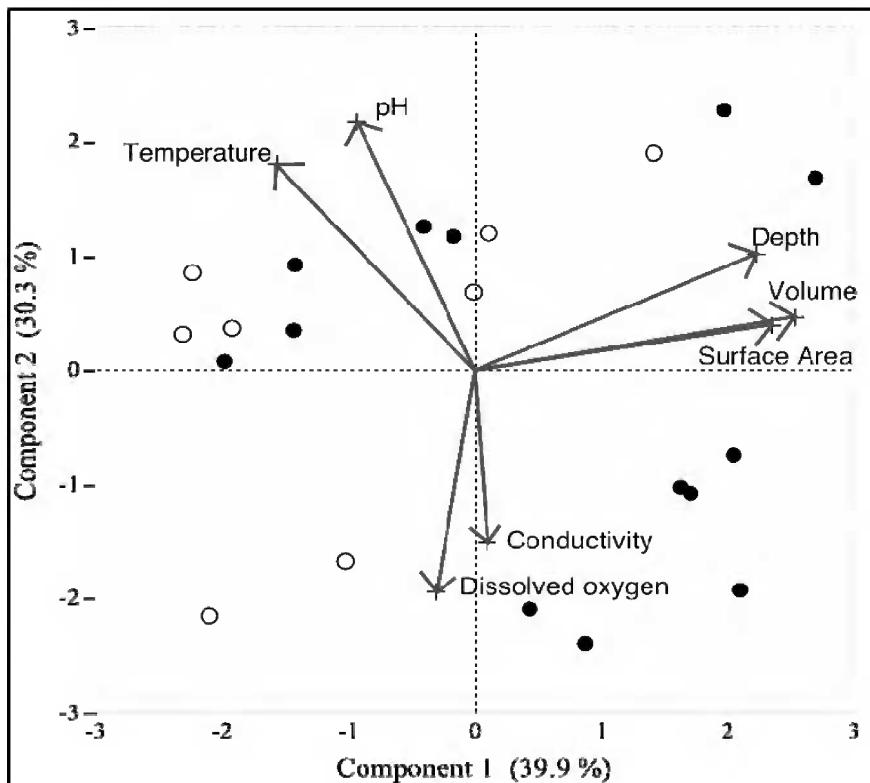
The PRIMER BEST procedure (Clarke & Ainsworth 1993) identified the combination of mean water quality and habitat variables for each pool, which best rank-correlated with clam shrimp abundances. These best correlating environmental variables are likely to be those that are most important in defining clam shrimp abundance. Prior to BEST analysis, environmental variables were normalized to the maximum value encountered (Olsgard *et al.* 1997, Clarke & Warwick 2001) and draftsman plots were created to determine which variables were highly correlated with each other (i.e., 95% or greater, Bob Clarke, Plymouth Marine Laboratory UK pers. comm.). Data were then \log_{10} transformed to enhance a linear relationship between variables and finally standardized to account for different variable scales (Clarke & Warwick 2001).

A canonical discriminate analysis (CDA) was then used (JMP Pro 10, SAS Institute Inc.) to determine which environmental variables best described the variation between groups (presence / absence of *P. badia*; see below). Bivariate regressions were then made to describe relationships between *P. badia* abundance, estimated fitness and habitat pH. Fitness was estimated from the size of the carapace, which is directly related to the number of resting eggs per clutch in female clam shrimp (Weeks *et al.* 1997).

RESULTS

Of the 21 pools studied on Holland and Dingo Rocks, 13 contained clam shrimp populations. Pools with and without *P. badia* had different abiotic conditions. Pool depth was related to pool volume and surface area (shown as factor loadings clustering on the loading plot; Fig. 1), which is expected because of the common formula used to derive pool volume. Examined individually, pH was the only abiotic parameter that differed significantly between the two groups (Table 1). Pools containing *P. badia* typically had lower pH than those without clam shrimp. Pools containing *P. badia* had overlapping ranges of all variables with pools lacking *P. badia*. The water temperature of the pools without *P. badia* was also higher, but not significantly so ($p=0.06$). Pool volume, surface area, conductivity, and TDS were higher in the pools that had *P. badia* populations, albeit not significantly.

Mean depth was the most important sole environmental variable explaining clam shrimp abundance according to the BEST analysis (Spearman Rank correlation: rho = 0.375). When pH was added to this model, this water quality variable further helped to explain clam shrimp distribution at rho = 0.413.



	Principal Component 1	Principal Component 2
Temperature	-0.35*	0.46*
Dissolved Oxygen	-0.07	-0.49*
pH	-0.21	0.55*
Depth	0.49*	0.26
Surface Area	0.52*	0.10
Conductivity	0.02	-0.38*
Volume	0.56*	0.12

Figure 1. PCA of pool environmental variables. Length of vector indicates strength of correlation between variable and component axes. Asterisks indicate significant correlation of the component with the original variable (* $p<0.05$). Pools with *P. badia* present are filled circles. Pools without *P. badia* are empty circles.

Table 1. Habitat characteristics of 21 total pools with *P. badia* present (n=13) and absent (n=8). Bold type indicates statistically significant difference ($p<0.05$) between pool environmental variable with and without *P. badia*.

	Pools without <i>P. badia</i>				Pools with <i>P. badia</i>				F-ratio	p-value
	Mean	SE	Max	Min	Mean	SE	Max	Min		
Temperature (°C)	21.2	0.41	26.1	17.3	20.3	0.25	25.8	17.2	3.95	0.061
Conductivity (mS/cm)	0.24	0.03	0.47	0.06	0.27	0.04	0.93	0.04	0.07	0.799
Dissolved oxygen (%)	113	2.75	138	97.3	109	1.60	141	88.9	1.46	0.243
pH	7.09	0.17	9.03	5.91	6.64	0.13	8.57	5.53	4.39	0.049
Depth (mm)	30.7	5.36	70.7	4.33	39.0	2.48	68.3	17.7	2.56	0.126
Volume (L)	136	41.3	420	1.71	276	59.9	930	24.9	2.83	0.109
Surface area (m ²)	7.32	1.41	14.2	0.75	12.2	2.14	28.5	1.98	2.75	0.114

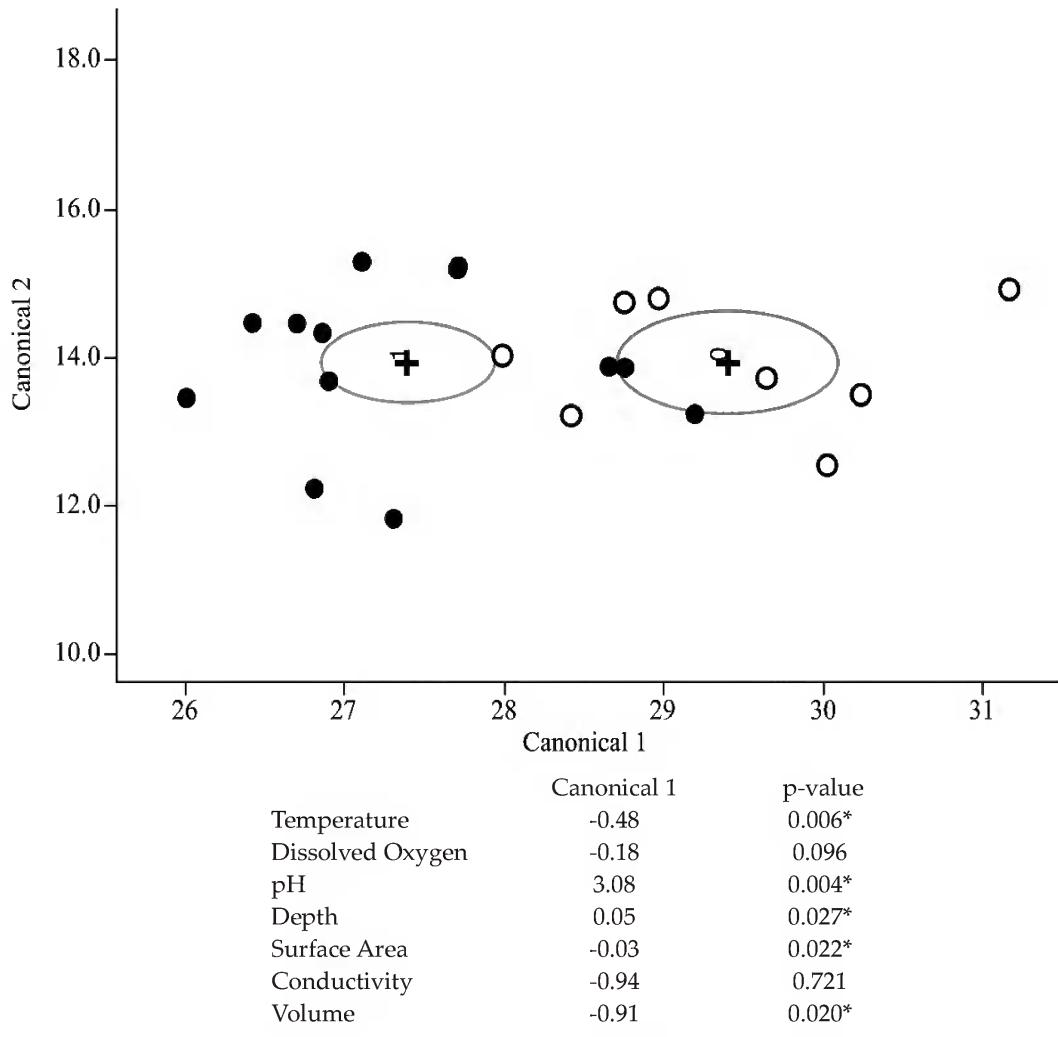


Figure 2. Results of a canonical discriminate analysis (CDA) on all seven dependent variables using data from Holland and Dingo outcrops only. Pools without *P. badia* present are empty circles; pools with *P. badia* present are filled circles. Canonical correlation 1 explains ~100% of the differences between present/absent pools. Ellipses show the means of the centroids of *P. badia*-present pools and *P. badia*-absent pools. Asterisks indicate significant correlations of the canonical scores with each of the original variables (* $p<0.05$).

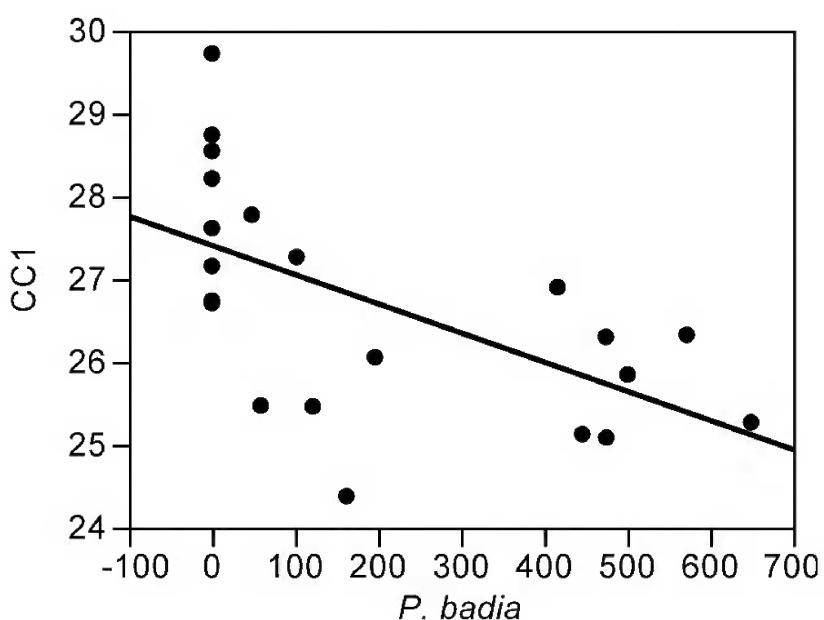


Figure 3. Regression of CC1 on the quantity of *P. badia* present in all pools. Canonical 1 (consisting largely of volume, depth, and surface area) is negatively correlated with the quantity of *P. badia* ($p=0.0052$).

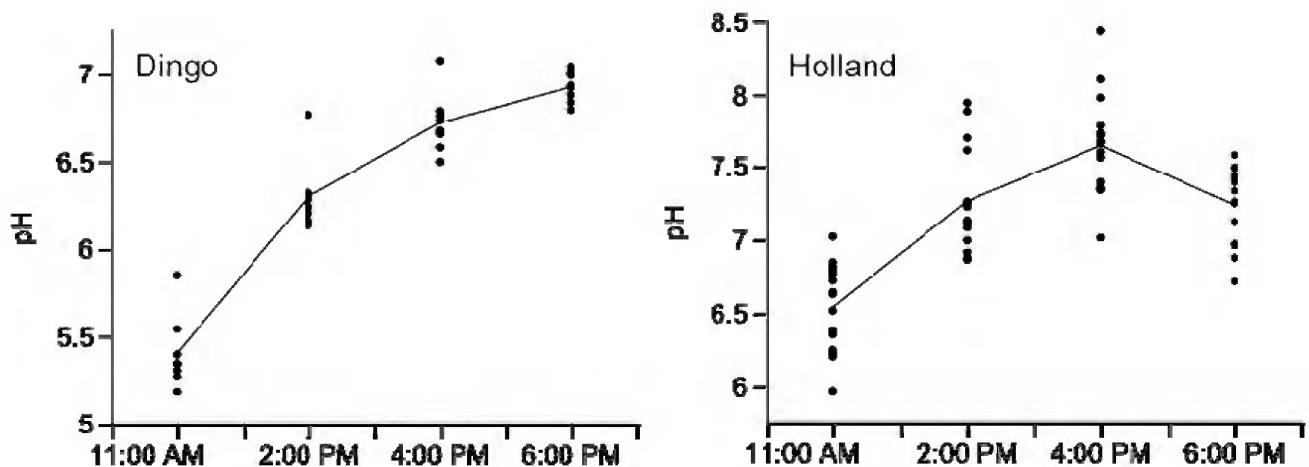


Figure 4. Diurnal variation in pH levels in pools on Dingo and Holland Rocks.

The CDA correctly classified 17 of 21 pools in its assignment of pools into groups that either had *P. badia* or not, or 81% of the total pools in this comparison (Fig. 2). The first canonical correlation (CC1) explained ~100% of the important variation that differed between pools with and without *P. badia*. Five original dependent variables were correlated strongly with CC1: temperature, depth, and surface area were negatively correlated with CC1, while volume and pH were significantly positively correlated with CC1 (Fig. 2). Volume, depth, and surface area are all measures describing pool size. Temperature and pH are variable that are closely associated and influenced by pool size, which suggests that CC1 is mainly describing the size of the pools. This 'pool size' variable is negatively correlated with the quantity of *P. badia* (Fig. 3). Figure 4 displays the diurnal variability of pH in pools on Dingo and Holland rocks.

DISCUSSION

Our study confirms that temporary rock pools are highly variable environments (Bayly 1982, Williams 2001). To survive this environment, pool inhabitants must cope with extended periods of drought between wet phases as well as the widely variable conditions throughout the inundation phase.

There is a wealth of literature available that quantifies the habitat requirements for large brachiopods to break dormancy (Moore 1963, Belk 1977, Brendonck 1996, Schönbrunner & Eder 2006). The information available regarding the maintenance of populations of clam shrimp mainly suggests that the size of the pools is of key importance (Kiflawi *et al.* 2003 & Jocqué *et al.* 2007b). Frequently, clam shrimp nauplii will hatch from resting eggs, but then the population will crash before they have reached maturity (Jocqué *et al.* 2007b). Much of the available information regarding hatching or sustaining populations is focused on the range of a single parameter (i.e., only temperature or pH; Belk 1977, Scott & Grigarick 1979, Mitchell 1990, Schönbrunner &

Eder 2006). However, by combining all parameters into a multivariate BEST analysis, we showed that pool depth combined with pH best explained *P. badia* abundance in temporary outcrop pool habitats. A canonical discriminate analysis confirmed pool depth and pH as the most vital explanatory variables, while additionally implicating volume, surface area, and temperature as important habitat variables. Temperature was negatively correlated with volume, depth, and surface area, as might be expected: as pool sizes increase, maximum pool water temperatures decrease because larger pools can be more resistant to temperature change. The sampling times used in this analysis were from the warmest parts of the diurnal cycle, and thus the larger volume pools should have been more resistant to warming, explaining the negative correlation.

The environmental variables that described pool morphology were all positively correlated with one another and with CC1. Canonical correlation 1 correctly predicted which pools contained *P. badia* 81% of the time, illustrating that pool morphology was a key habitat characteristic for *P. badia* abundance. This may well be because pools that are on the more ephemeral end of the continuum evaporate before clam shrimp populations have reached sexual maturity.

The apparent association between pH and the presence of *P. badia* (Table 1) is likely an artifact of the sampling regime (i.e., pH values used in this analysis were only from the middle of the day and thus do not take into account the significant diurnal change observed; Fig. 4). It is possible that the variability of pH, like temperature is associated with the size of the pool and this is why it appears significant here. Otherwise it is not obvious why such a subtle difference in mean pH between the two groups (0.45) would have an impact on *P. badia* populations. More information is necessary to determine the significance of this observation.

Clam shrimp species previously reported from these pools were *Eulimnadia dahli* Sars, 1896 and *Paralimnadia badia* (Timms 2006, Weeks *et al.* 2006). Whether these

genera never coexist within the same pool or whether one succeeds the other in the same pools is still unknown. Preliminary evidence suggests that *P. badia* may predominate in pools in the winter (rainy) season, while *E. dahli* may be more common in the summer (Timms 2006).

These data represent the results of an observational and not a manipulative study and so can only suggest a potential relationship between the above variables, not necessarily a direct causal relationship. There may also be other factors beyond pool morphology that could affect the distribution of this species. It is possible that clam shrimp had not yet dispersed to the non-*P. badia* pools, although this scenario is unlikely considering the proximity of the pools to each other on each outcrop. Overflow and wind-mediated propagule dispersal have been shown to be extremely effective in temporary pool metacommunities (Brendonck & Riddoch 1999, Vanschoenwinkel *et al.* 2008a, Vanschoenwinkel *et al.* 2008b). Another possibility is that the presence of a predator excluded *P. badia* from some pools and not others, although this seems unlikely. Some clam shrimp were consumed by predacious water beetle larvae (Dytiscidae) during sampling, but this was a rare occurrence in our observations. Furthermore, in every pool in which these predacious larvae were present, *P. badia* was also present. Additionally, 81% of pools that harboured anuran larvae also had *P. badia*. Our sampling was not exhaustive enough to prove that no predator had an effect on *P. badia* populations, but simply suggests that we did not observe such a phenomenon during our sampling period.

Generally, there is thought to be a continuum of factors structuring communities in habitats ranging from permanent freshwater bodies to temporary freshwater environments (Wellborn *et al.* 1996). Some work has suggested that predation is the dominant structuring force in the most permanent communities while competition is more powerful in structuring pools that are less permanent (Wellborn *et al.* 1996, Wilbur 1987). Indeed, priority effects may play a role in early colonizers monopolizing particular pools (De Meester *et al.* 2002, Jocqué *et al.* 2010).

Another factor that may affect the habitat quality of *P. badia* is dryland salinity. Extensive land clearing in the region has resulted in increased salinities in many aquatic habitats (Anon 1996, National Land and Water Resources Audit 2001). Dust and saline solutes from salt flats around the rock outcrops are likely to be both more alkaline and also more buffered. Some outcrop pools are also showing higher alkalinity through increased bicarbonate concentrations than would be expected from rainfall interaction with acidic granite rock (Pinder *et al.* 2005).

Pool morphology appears to influence the presence of *P. badia* in temporary rock pools. Temperature may also be an influential factor, especially as it is correlated with the size of the pools. Many of these outcrops are already functioning as islands in an ecological desert that is the mono-agricultural Wheatbelt landscape. Consequently, loss of these island habitats to clam shrimp at a local scale may lead to a significant threat to sustained existence for clam shrimp at a more regional scale.

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REFERENCES

ANONYMOUS 1996. Western Australian Salinity Action Plan. Government of Western Australia, Perth.

BAYLY I A E 1982. Invertebrate fauna and ecology of temporary pools on granite outcrops in southern Western Australia. *Australian Journal of Marine and Freshwater Research* **33**, 599–606.

BELAJAL L, KIERCKENS K & MERTENS J 2007. Pheromones inhibit the hatching of diapausing Anostraca (Crustacea: Branchiopoda). *Animal Biology* **57**, 1–9.

BENVENUTO C, CALABRESE A, REED S K & KNOTT B 2009. Multiple hatching events in clam shrimp; implications for mate guarding behavior and community ecology. *Current Science* **96**, 130–136.

BARON J S, LAFRANCOIS T & KONDRAEFF B C 1998. Chemical and biological characteristics of desert rock pools in intermittent streams of Capitol Reef National Park, Utah. *Great Basin Naturalist* **58**, 250–264.

BELK D 1977. Zoogeography of the Arizona fairy shrimps (Crustacea: Anostraca). *Journal of the Arizona Academy of Science* **12**, 70–78.

BISHOP J A 1967. Some adaptations of *Limnadia stanleyana* King (Crustacea: Branchiopoda: Conchostraca) to a temporary freshwater environment. *Journal of Animal Ecology* **36**, 599–609.

BOIX D, SALA J, QUINTANA X D & MORENO-AMICH R 2004. Succession of the animal community in a Mediterranean temporary pond. *Journal of the North American Benthological Society* **23**, 29–49.

BRENDONCK L 1996. Diapause, quiescence, hatching requirements: What we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). *Hydrobiologia* **320**, 85–97.

BRENDONCK L, CENTENO M D & PERSOOONE G 1996. The influence of processing and temperature conditions on hatching of resting eggs of *Streptocephalus proboscideus* (Crustacea: Branchiopoda: Anostraca). *Hydrobiologia* **320**, 99–105.

BRENDONCK L & RIDDOCH B J 1999. Wind-borne short-range egg dispersal in anostracans (Crustacea: Branchiopoda). *Biological Journal of the Linnean Society*, **67**, 87–95.

BRENDONCK L & DE MEESTER L 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. *Hydrobiologia* **491**, 65–84.

BRENDONCK L & RIDDOCH B J 2000. Egg bank dynamics in anostracan desert rock pool populations (Crustacea: Branchiopoda). *Archiv Fur Hydrobiologie* **148**, 71–84.

CHAN M A, MOSER K, DAVIS J M, SOUTHAM G, HUGHES K & GRAHAM T 2005. Desert potholes: Ephemeral aquatic microsystems. *Aquatic Geochemistry* **11**, 279–302.

CLARKE K R & AINSWORTH M 1993. A method for linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205–219.

CLARKE K R & WARWICK R M 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd edn, Plymouth Marine Laboratory, Plymouth.

COMMONWEALTH of AUSTRALIA, BUREAU OF METEOROLOGY. 2011. Lake Grace Comparison and Hyden climate averages, http://www.bom.gov.au/climate/averages/tables/ca_wa_names.shtml. Accessed: 26 September 2011.

DE MEESTER L, GÓMEZ A, OKAMURA B & SCHWENK K 2002. The Monopolization Hypothesis and the dispersal-gene flow paradox in aquatic organisms. *Acta Oecologica* **23**, 121–135.

DUMONT H J & NEGREA S V 2002. Introduction to the class Branchiopoda, *Guides to the Identification of Microinvertebrates of the Continental Waters of the World* 19, Backhuys, Leiden.

HALSE S A, RUPRECHT J K & PINDER A M 2003. Salinisation and prospects for biodiversity in rivers and wetlands of southwest Western Australia. *Australian Journal of Botany* **51**, 673–688.

JOCQUÉ M, RIDDOCH B J & BRENDONCK L 2007a. Successional phases and species replacements in freshwater rock pools: towards a biological definition of ephemeral systems. *Freshwater Biology* **52**, 1734–1744.

JOCQUÉ M, GRAHAM T & BRENDONCK L 2007b. Local structuring factors in ephemeral freshwater rock pools and the influence of more permanent water bodies in the region. *Hydrobiologia* **592**, 271–280.

JOCQUÉ M, VANSCHOENWINKEL B & BRENDONCK L 2010. Anostracan monopolization of early successional phases in temporary waters? *Fundamental and Applied Limnology* **176**, 127–132.

KHALAF A N & AL-JAAFERY A R 1985. Hatching conditions for *Eucypris virens* (Conchostraca: Crustacea) from Iraq. *Hydrobiologia* **123**, 263–264.

KIFLAWI M, EITAM A & BLAUSTEIN L 2003. The relative impact of local and regional processes on macro-invertebrate species richness in temporary pools. *Journal of Animal Ecology* **72**, 447–452.

KULLER Z & GASITH A 1996. Comparison of the hatching process of the tadpole shrimps *Triops cancriformis* and *Lepidurus apus lubocki* (Notostraca) and its relation to their distribution in rain-pools in Israel. *Hydrobiologia* **335**, 147–157.

LINDSAY M D A, JARDINE A, JOHANSEN C A, WRIGHT A E, HARRINGTON S A & WEINSTEIN P 2007. Mosquito (Diptera: Culicidae) fauna in inland areas of south-west Western Australia. *Australian Journal of Entomology* **46**, 60–64.

MEINTJES S, SEAMAN M T & KOK D J 1994. Duration of inundation and change in physical and chemical characteristics of small temporary pools in South Africa. *Hydrobiologia* **281**, 79–90.

MITCHELL S A 1990. Factors affecting the hatching of *Streptocephalus macrourus* Daday (Crustacea; Eubranchiopoda) eggs. *Hydrobiologia* **194**, 13–22.

MOORE W G 1963. Some interspecies relationships in Anostraca populations of certain Louisiana ponds. *Ecology* **44**, 131–139.

MOSSIN J 1986. Physicochemical factors inducing embryonic development and spring hatching of the European fairy shrimp *Siphonophanes grubei* (Dybowsky) (Crustacea: Anostraca). *Journal of Crustacean Biology* **6**, 693–704.

NATIONAL LAND and WATER RESOURCES AUDIT 2001. *Australian Dryland Salinity Assessment 2000: Extent, Impacts, Processes, Monitoring and Management Options*. Land and Water Australia, Canberra, Australia.

OLSGARD F, SOMERFIELD P J & CARR M R 1997. Relationships between taxonomic resolution and data transformations in analyses of a macrobenthic community along an established pollution gradient. *Marine Ecology Progress Series* **149**, 173–181.

PAJUNEN V I & PAJUNEN I 2007. Habitat characteristics contributing to local occupancy and habitat use in rock pool *Daphnia* metapopulations. *Hydrobiologia* **592**, 291–302.

PHILIPPI T E, SIMOVICH M A, BAUDER E T & MOORAD J A 2001. Habitat ephemerality and hatching fractions of a diapausing Anostracan (Crustacea: Branchiopoda). *Israel Journal of Zoology* **47**, 387–395.

PINDER A M, HALSE S A, MCRAE J M, & SHIEL R J 2005. Occurrence of aquatic invertebrates of the wheatbelt region of Western Australia in relation to salinity. *Hydrobiologia* **543**, 1–124.

PINDER A M, HALSE S A, SHIEL R J & MCRAE J M 2000. Granite outcrop pools in south-western Australia: foci of diversification and refugia for aquatic invertebrates. *Journal of the Royal Society of Western Australia* **83**, 149–161.

PRIMER-E Ltd 2006. PRIMER. 6.1.5, Plymouth Marine Laboratory, Plymouth.

RAMSING N B, KUHL M & JORGENSEN B B 1993. Distribution of sulfate reducing bacteria, O_2 and H_2S in photosynthetic biofilms determined by oligonucleotide probes and microelectrodes. *Application of Environmental Microbiology* **59**, 3840–3849.

RICHTER S & TIMMS B V 2005. A list of the recent clam shrimps (Crustacea: Laevicaudata, Spinicaudata, Cyclesterida) of Australia, including a description of a new species of *Eucypris*. *Records of the Australian Museum* **57**, 341–354.

SAS Institute Inc. 2012. JMP Version 10.0. www.jmp.com

SCHOLNICK D A 1994. Seasonal variation and diurnal fluctuations in ephemeral desert pools. *Hydrobiologia* **294**, 111–116.

SCHÖNBRUNNER I M & EDER E 2006. pH-related hatching success of *Triops cancriformis* (Crustacea: Branchiopoda: Notostraca). *Hydrobiologia* **563**, 515–520.

SCOTT S R & GRIGARICK A A 1979. Laboratory studies of factors affecting egg hatch of *Triops longicaudatus* (Leconte) (Notostraca: Triopsidae). *Hydrobiologia* **63**, 145–152.

SIMOVICH M A & HATHAWAY S A 1997. Diversified bet-hedging as a reproductive strategy of some ephemeral pool Anostracans (Branchiopoda). *Journal of Crustacean Biology* **17**, 38–44.

TIMMS B V 2006. The large branchiopods (Crustacea: Branchiopoda) of gnammas (rock holes) in Australia. *Journal of the Royal Society of Western Australia* **89**, 163–173.

VANSCHOENWINKEL B, GIELEN S, SEAMAN M & BRENDONCK L 2008. Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos* **117**, 125–134.

VANSCHOENWINKEL B, GIELEN S, VANDEWAERDE H, SEAMAN M & BRENDONCK L 2008. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography*, **31**, 567–577.

WEEKS S C, MARCUS V & ALVAREZ S 1997. Notes on the life history of the clam shrimp, *Eulimnadia texana*. *Hydrobiologia* **359**, 191–197.

WEEKS S C, ZOFKOVA M & KNOTT B 2006. Limnadiid clam shrimp distribution in Australia (Crustacea: Branchiopoda: Spinicaudata). *Journal of the Royal Society of Western Australia* **89**, 155–161.

WELLBORN G A, SKELLY D K & WERNER E E 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27**, 337–363.

WITHERS P C 2000. Overview of granite outcrops in Western Australia. *Journal of the Royal Society of Western Australia* **83**, 103–108.

WILBUR H M 1987. Regulation of structure in complex systems: experimental temporary pond communities. *Ecology* **68**, 1437–1452.

WILLIAMS D D 2001. *The Ecology of Temporary Waters*. The Blackburn Press, Caldwell, NJ.

WILLIAMS W D 1968. *Australian Freshwater Life: The invertebrates of Australian inland waters*. Sun Books, Melbourne, Australia.

YORK MAIN B 1997. Granite outcrops: A collective ecosystem. *Journal of the Royal Society of Western Australia* **80**, 113–122.